# **FORAGES**

# **Developmental Dynamics of Forage Chicory**

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### **ABSTRACT**

Most studies on forage chicory (Cichorium intybus L.) are empirical, and very little information exists regarding the growth of chicory as it relates to development, productivity, persistence, and stand age. Development of uncut 'Grasslands Puna' chicory was studied in southern West Virginia on previously established plots at the Scott Farm in 1997 and 1998 and on 1-yr-old plantings at the Plumley Farm in 1998 and 1999. Chicory developmental parameters were modeled as a function of growing degree days (GDD) from Calendar Day 90 using a base of 5°C. On average, only 58% of the chicory plants became reproductive in any single growing season or location after the establishment year. Mean time to initiation of bolting and first open flower occurred consistently at approximately 400 and 1030 GDD, respectively, across locations and years. The indeterminate meristem of vegetative plants continuously produced leaves of relatively uniform mature area throughout the growing season. In comparison, the determinate meristem of reproductive plants rapidly expressed progressively smaller leaves on the main stem from initiation of bolting only until the time of first open flower. The developmental data herein create a framework with which to begin optimizing strategies for pasture and livestock grazing management of forage chicory.

CHICORY is a forage that meets the nutritional needs of grazing livestock in temperate regions (Barry, 1998). Chicory is considered a weed by many because it is commonly found along roadsides and in waste areas throughout the eastern USA (Smith and Capelle, 1992). However, chicory has agronomic value due to its ability to produce high quality forage even during maritime winters (e.g., New Zealand) or periods of summer drought (O'brien, 1955). Its taproot can break up shallow subsoils (Clapham et al., 1962). Belesky et al. (1996) showed that chicory can increase herbage mass available during midsummer relative to cool season grass-legume pastures.

Chicory is a perennial herb that produces a rosette following seeding (Rumball, 1986). The plant is dormant during cold winter months and, if vernalized, bolts under long days during the subsequent growing season (Gianquinto and Pimpini, 1989). Although flowering stems produce leaves, leaf size decreases progressively from stem base to apex (Doorenbos and Riemens, 1959).

Chicory cultivars such as Grasslands Puna, which was recently released in New Zealand, sparked interest with greater agronomic potential than common weedy wild

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types (Rumball, 1986). Interest in chicory spread to the USA, and trials were conducted to determine its utility there (Volesky, 1996; Jung et al., 1996). Jung et al. (1996) evaluated the performance of Grasslands Puna under different clipping regimes and observed that it had superior seedling vigor and a competitive advantage over orchardgrass (Dactylis glomerata L.). Three clippings of vegetative Grasslands Puna produced a total forage mass of 7.5 Mg ha<sup>-1</sup> during the seeding year. Clark et al. (1990b) found that in reproductive chicory, main stems can make up as much as 50% of the dry matter and have low acceptability to livestock. In the same study, Friesian bulls grazing morphologically differentiated Grasslands Puna in the reproductive stage produced acceptable weight gains as long as chicory leaf allowances were sufficient to meet nutritional requirements.

Collins and McCoy (1997) observed that chicory herbage yields increased linearly with N rates between 0 and 200 kg N ha<sup>-1</sup>. High N rates (200 kg ha<sup>-1</sup>) were associated with declining plant density and residual regrowth (Clark et al., 1990a). Belesky et al. (2000) showed that chicory growth responded to rates up to 480 kg N ha<sup>-1</sup> and experienced a similar decline in stand over time. To maintain production of high-value forage in reproductive plants, management strategies have focused on grazing or clipping stems during the early growing season to encourage axillary vegetative shoot development (Clark et al., 1990a; Moloney and Milne, 1993; Li et al., 1994; Li et al., 1997b).

A study of harvest frequency and N rates produced total annual dry matter yields of 2187, 3262, 4869, and 6402 kg ha<sup>-1</sup> for cutting intervals of 1, 2, 4, and 8 wk, and dry matter yields of 3029, 3910, and 5684 kg ha<sup>-1</sup> for N rates of 0, 50, and 200 kg  $ha^{-1}$  (Clark et al., 1990a). Li et al. (1997c) related herbage production, contrasting root size, root carbohydrate reserves, and defoliation intensity with biomass allocation and regrowth of Grasslands Puna, concluding that cutting frequency had more impact than cutting intensity. Residual regrowth and plant density decreased on plots treated with 200 kg N ha<sup>-1</sup> and cut to ground level at 1- or 2-wk intervals (Clark et al., 1990a). Grazing late into the autumn reduced chicory populations by 27% in the following spring (Li et al., 1997b). In a grazing study over 4 yr, Li et al. (1997a) observed plant densities of 66 and 68 plants m<sup>-2</sup> in Years 1 and 2 decreasing to 49 and 24 plants  $m^{-2}$  in Years 3 and 4.

**Abbreviations:** GDD, growing degree days; PAR, photosynthetically active radiation.

The potential utility of chicory as a forage crop can be enhanced by a number of approaches. At the very least, leaf production before and during bolting, seasonal carbohydrate dynamics, flowering and seed set rate, and success in reseeding will have to be predictable and balanced to ensure stable forage production and persistence. This knowledge may be the result of compiling numerous empirical studies and/or development of mathematical models that describe growth and development of the plant in relation to production, quality, and persistence. The objectives of this study were to (i) develop a practical understanding of chicory development in relation to the driving parameters of temperature and available light, (ii) relate plant development in terms of rates of leaf initiation and loss to forage productivity, and (iii) assess chicory utility as a forage based on its development and productivity during the growing season.

#### **MATERIALS AND METHODS**

Chicory development was monitored at two sites in southern West Virginia. Grasslands Puna chicory was established in small plots at the Scott Farm (38°N, 81°W; 850 m above sea level) in June 1993. Soils on the gently sloping site were a Ramsey fine-loam (siliceous mesic Typic Hapludult). Establishment and management of these plots through the fall of 1996 were described in detail by Belesky et al. (1999).

The plots were predominantly a mixture of chicory, white clover (*Trifolium repens* L.), and orchardgrass when harvests were discontinued in 1997 to allow study of chicory development in undefoliated swards. Annual spring fertilizer applications (35, 80, and 150 kg ha<sup>-1</sup> N, P, and K) continued through 1998. A total of 72 single-crowned plants were selected within the plots in a stratified random manner in the spring of 1997. Multicrowned plants were avoided due to the difficulty of differentiating them from two or more closely entwined individual plants. Selected plants were permanently marked with a numbered flag and a 5-cm-diam. polyvinyl chloride ring. Leaves (nodes) were numbered with permanent black marker to permit tracking of newly formed leaves on the main axis each time that a plant was observed. Growth stage (vegetative rosette, bolting, or flowering) was also recorded at each observation

Sampling opportunities were dictated, in part, by available help and access to producer-owned pasture. All 72 plants were observed weekly from late April through September in 1997. Biweekly observations of surviving plants were made in 1998 to reduce sampling time while still capturing leaf population and growth stage dynamics. Observations on the Scott Farm ceased at the end of July 1998 due to termination of a lease agreement. Major developmental milestones (bolting and first flower) were completed by this time. Weekly monitoring of leaf senescence and plant height on all 72 plants and of branch and flower development on four marked reproductive plants occurred in 1997 only. A six-stage scale was created to describe flower development: 0, green bud; 1, bullet shaped; 2, fully open; 3, senesced petals; 4, abscised petals; and 5, brown seed.

A second area for chicory study was established at the Plumley Farm approximately 7 km east of the Scott Farm. Soil, slope characteristics, and elevation were similar at both sites. Plots at the Plumley Farm were used primarily for an evaluation of the effect of forage removal on chicory development and survival, which will be presented in a separate paper. Portions of these plots, however, remained uncut for all or

half of the year after establishment, and thus provided an opportunity to compare development patterns of uncut chicory across locations and stand ages.

Plot areas were established by killing an established pasture with glyphosate [N-(phosphonomethyl)glycine] in midspring and then rototilling to a depth of approximately 10 cm. The 3.6- by 12.2-m plots were hand-sown with Grasslands Puna chicory at a rate of 5 kg ha<sup>-1</sup> pure live seed. Orchardgrass ('Benchmark') and white clover ('Huia') were then oversown with a Brillion seeder at rates of 15 and 1 kg ha<sup>-1</sup>, respectively. One set of plots was sown on 24 June 1997, and a second set was sown on 19 May 1998. Plots established in 1997 received no fertility amendments during the establishment year, and the initial growth was grazed to an approximate 5-cm stubble by feral deer in early fall. Plots established in 1998 were amended with a total of 67, 69, and 112 kg ha<sup>-1</sup> N, P, and K in a split application during the year of establishment, and the initial growth was harvested with a flail mower (10-cm stubble) in early August to control weeds. After the establishment year, all plots received annual midspring applications of 30.5, 67.5, and 112 kg ha<sup>-1</sup> N, P, and K.

Forty plants were selected at random each year for observation. Individual chicory plants established in 1997 were marked and observed in 1998, and plants established in 1998 were marked and observed in 1999. The marked plants were assessed biweekly to determine time of bolting (1998 and 1999) and initial flowering (1999) along with nodal expression rates (1998 and 1999). Fifteen vegetative and 15 reproductive plants were collected monthly in 1999 (from the plots established in 1998) to determine the relationships among leaf size (area), insertion point, and time of year.

Temperature and light data were collected at the sites using portable weather stations. Cumulative photosynthetically active radiation (PAR) and GDD, using a base of 5°C, were calculated beginning on 30 March (Calendar Day 90) of each year before the beginning of active spring growth. The potential utility of cumulative GDD, cumulative PAR, calendar day, and daylength (hours of daylight day<sup>-1</sup>) as consistent predictors of bolt and flower initiation across locations and years was assessed using completely randomized analysis of variance with protected Duncan's multiple-range tests (P < 0.05) (SAS, 1985). Developmental parameters were modeled as functions of cumulative GDD using NLIN and REG procedures of SAS (Freund and Littell, 1991). To evaluate the regression models in terms of the plant population response to GDD, the models were fit to mean values at each sample time rather than to the raw data. This approach removes the pure error due to variation within sample dates and generates a coefficient of determination that gives a better sense of what the model achieved in terms of the average population response (Draper and Smith, 1981). Bars representing pooled standard errors of the mean are included on regression plots to indicate variability in the raw data. Models of cumulative node formation of main stems (Scott Farm in 1997 and Plumley Farm in 1998 and 1999) and leaf senescence (Scott Farm in 1997) were created. First derivatives of these regression models were then used to determine continuous rates of node formation and leaf senescence. Finally, net rates of main stem leaf formation were determined as the difference between rates of node formation and leaf senescence across the season (Scott Farm in 1997 only).

### **RESULTS**

The growing season of 1997 was somewhat cooler than the long-term average for the area (Table 1). Tem-

		Mean monthly temperature					Total monthly precipitation				
	Scott Farm		Plumley Farm		30-yr mean†	Scott Farm†		Plumley Farm		30-yr mean†	
	-	°C				mm					
	1997	1998	1998	1999		1997	1998	1998	1999		
Jan.	-1.30	-1.29	1.74	1.01	-1.60	66	122	98	113	74	
Feb.	2.90	0.68	2.00	0.95	0.10	52	126	72	65	75	
Mar.	6.50	2.64	3.84	1.71	5.60	163	96	89	58	86	
Apr.	7.90	10.29	10.50	11.49	10.70	67	119	_	84	87	
May	12.00	16.38	16.29	15.48	15.30	108	192	169	54	101	
June	17.60	18.61	18.36	18.91	19.00	119	178	180	44	98	
July	20.90	20.59	20.41	22.01	20.90	110	114	87	86	119	
Aug.	18.90	-‡	20.50	19.71	20.40	83	39	46	62	86	
Sept.	16.50	_	19.20	16.49	17.10	37	48	68	96	85	
Oct.	10.80	_	11.88	10.49	11.30	23	38	34	60	73	
Nov.	3.10	_	6.49	8.04	6.30	75	67	60	62	76	
Dec.	0.00	_	2,32	1.60	1.10	56	110	101	60	82	

Table 1. Mean monthly temperatures and precipitation for the Scott and Plumley Farms from 1997 to 1999.

peratures in 1998 and 1999 were closer to the long-term mean. Temperature differences among the years are reflected in the patterns of GDD accumulation (Fig. 1A). Precipitation was well distributed throughout the growing season at near-normal levels in 1997 and 1998 but was below normal during most of the 1999 growing season (Table 1). Total PAR accumulated in a linear fashion from Day 90 through late summer each year (data not shown), reflecting the increased daylight hours in this period (Fig. 1B). The pattern of GDD accumula-

tion lagged behind that of PAR and did not reach a linear phase of accumulation until late spring (Fig. 1A).

Each year in early spring, all chicory plants had a rosette growth form composed of a whorl of 5 to 15 leaves. The first visual indication that a plant would become reproductive was elongation of the main stem (bolting). Fifty-six percent of the marked plants bolted during the 1997 growing season at Scott Farm; the rest (44%) remained vegetative (Table 2). In 1998, 27 (52%) of the 52 surviving marked plants bolted. The fraction of the population bolting in 1-yr-old stands at the Plumley

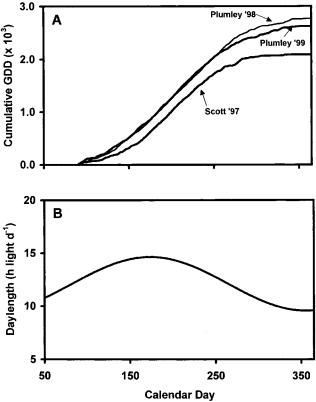


Fig. 1. (A) Cumulative growing degree days (GDD) (base 5°C) from 30 March (Calendar Day 90) through 31 December at the Scott Farm in 1997 and at the Plumley Farm in 1998 and 1999. The partial data set for Scott Farm in 1998 (not shown) was similar to the 1998 Plumley Farm. (B) Daylight hours per day at 37°45′N lat.

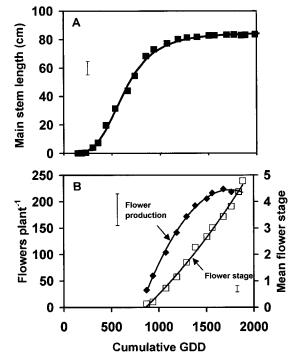


Fig. 2. Development of reproductive chicory plants at Scott Farm in 1997. (A) Mean main-stem length (n=40 plants). The line represents the regression equation  $\{y=84.6/[1+(x/621.5)]^{-3.98}-0.36 (R^2=0.92; P<0.001\}. (B) Mean flower production <math>(\diamondsuit; n=4 \text{ plants})$  and flower developmental stage  $(\diamondsuit; n=4 \text{ plants})$ . Lines represent regression equations for flower production  $(y=-0.0002x^2+0.87x-538.3; R^2=0.99; P<0.001)$  and flower stage  $(y=1.0\times10^{-6}x^2+0.0016x-2.13; R^2=0.99; P<0.001)$ . Error bars are the pooled standard error of the mean.

<sup>†</sup> Data from the National Weather Service Beckley, WV Station (37°45' N, 81°15' W; 850 m elevation).

<sup>‡</sup> Missing data.

Table 2. Mean cumulative growing degree days (GDD), cumulative photosynthetically active radiation (PAR), calendar day, and hours of daylight day<sup>-1</sup> at initiation of bolting in chicory. The number of marked chicory plants observed during the bolting period and the number that bolted is included.

Location	Year	No. of plants	<b>Cumulative GDD</b>	Cumulative PAR	Calendar day	Daylight
		monitored/bolting		Mol m <sup>−2</sup>		h day <sup>-1</sup>
Scott Farm	1997	72/40	401a*	2127a	157a	14.5a
Scott Farm	1998	52/27	426a	1472b	144b	14.3b
Plumley Farm	1998	40/22	392a	_	141bc	14.2b
Plumley Farm	1999	40/29	370a	1651b	136c	14.1c

<sup>\*</sup> Values within a column followed by the same letter are not significantly different as determined by Duncan's multiple range test (P = 0.05).

Table 3. Mean cumulative growing degree days (GDD), cumulative photosynthetically active radiation (PAR), calendar day, and hours of daylight day<sup>-1</sup> at first open chicory flower. The number of marked chicory plants observed during the flowering period and the number that flowered is included.

Location	Year	No. of plants†	<b>Cumulative GDD</b>	<b>Cumulative PAR</b>	Calendar day	Daylight
		monitored/flowering		$Mol m^{-2}$		h day <sup>-1</sup>
Scott Farm	1997	72/40	1082a*	3810a	205a	14.2b
Scott Farm	1998	43/23	1062a	2950b	190b	14.5a
Plumley Farm	1999	20/9	949a	3540a	181b	14.6a

<sup>\*</sup> Values within a column followed by the same letter are not significantly different as determined by Duncan's multiple range test (P = 0.05).

Farm was similar in 1998 (55%) but higher in 1999 (72%) (Table 2).

Time of bolting was not significantly different among locations and years when measured in GDD (mean time to bolting was 397 GDD) but differences did occur when time of bolting was related to calendar day, cumulative PAR, and hours of daylight day<sup>-1</sup> (Table 2). Main stems elongated quickly after bolting was initiated and eventually reached an average final height of 85 cm (Fig. 2A) when this trait was measured at the Scott Farm in 1997. Flower bud formation was first noticed at around 850 GDD (Fig. 2B). Mean time to first open flower was consistent among locations and years when measured in GDD (mean time to first flower was 1031 GDD) (Table 3). Flower production was monitored only at the Scott Farm in 1997 where, once initiated, flower production continued at a rapid pace until slowing at about 1400 GDD (Fig. 2B). Total flower production averaged 227 flowers plant<sup>-1</sup> (SE = 76; n = 4). Each bud opened for only a single day. Individual nodes produced up to four or more buds in sequence over a period of 4 to 8 wk. As a result, individual nodes supported buds ranging in maturity from Stage 0 (green buds) to Stage 5 (brown seeds) by midsummer. Mean flower stage progressed linearly from 0.1 at 850 GDD to 4.7 at 1900 GDD (Fig. 2B). The mean time to final open flower was 1570 GDD in 1997, the only year that this trait was measured.

Flower buds formed in the axils of the upper leaves of the main stem and primary branches (plants averaged eight primary branches plant<sup>-1</sup>; SE = 3; n = 4). The uppermost main-stem nodes produced flowers but no branches (Fig. 3). The middle third of the main stem nodes often supported primary branches, and thereby numerous flowers because flowers developed at nearly every branch node. The lower third of the main stem nodes on reproductive plants supported neither branches nor flowers.

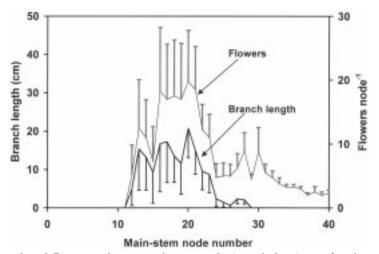


Fig. 3. Mean primary branch length and flower number per main stem node (n=4 plants) as a function of main stem node number on reproductive chicory plants at the Scott Farm in 1997. Flower number for each node includes those flowers supported directly by the main stem as well as those supported by the associated branch. Vertical bars are +1 SE of the mean for flowers and -1 SE of the mean for branch length.

<sup>†</sup> The number of plants monitored during flowering at the Scott Farm in 1998 is lower than the number monitored at bolting due to mortality. The number of plants monitored at the Plumley Farm in 1999 at flowering is lower than the number monitored at bolting because half of the plants were clipped after bolting for use in a companion study.

Detailed leaf formation and senescence data on both vegetative and reproductive plants were collected at the Scott Farm only in 1997 (Fig. 4A and 4B). The first census was conducted that year on 22 April (146 GDD). At that time, all plants had a rosette growth form, but the plants destined to bolt and flower had an average of 32% more leaves (13.4 vs. 10.1 nodes plant<sup>-1</sup>; P <0.001) than those that would remain vegetative. Reproductive plants displayed a burst of node expression as the main stem elongated in late spring. Reproductive plants added an average of 20 main stem nodes between initiation of bolting and first flower, significantly more (P < 0.001) than the eight nodes expressed by vegetative plants during this time span. Reproductive plants ceased node formation when flowering began in early summer, but vegetative plants continued forming new nodes in a near linear fashion throughout the growing season (Fig. 4A). The sigmoidal pattern of node expression in reproductive plants reflected an average total increase of 29 nodes plant<sup>-1</sup>, 23% greater (P < 0.001) than the average of 22 nodes expressed on vegetative plants during the 1997 growing season. The sigmoidal pattern of node expression in reproductive plants was also noted at the Plumley Farm in 1998 and 1999 (Fig. 5).

The oldest leaves of both reproductive and vegetative plants senesced continuously throughout the growing season (Fig. 4B). Reproductive plants had higher rates of leaf senescence than vegetative plants. Reproductive plants lost an average of 10 leaves before initiation of bolting, significantly (P < 0.001) more than the seven leaves lost from vegetative plants during that same time interval.

Net rate of main stem leaf formation was calculated to integrate the co-occurring processes of leaf formation (node expression) and senescence recorded at the Scott Farm in 1997 (Fig. 6). Reproductive plants had a substantial net loss of leaves in early spring as they underwent the metabolic and morphological transition to a reproductive form. Reproductive plants, however, quickly shifted from negative to positive rates of net leaf formation as bolting was initiated. Net formation rates reached peak levels of 0.03 main stem leaves GDD<sup>-1</sup> at approximately 550 GDD, soon after stem elongation (bolting) had begun. Net formation rates then gradually dropped back to negative values as the first flowers opened at around 1100 GDD. Net rates remained negative throughout the remainder of the growing season because leaf formation had ceased and the lower main stem leaves continued to senesce as reproductive structures matured. Vegetative plants also exhibited a net loss of leaves early in the season but had positive, yet relatively low, net leaf formation rates beginning from about 500 until 2000 GDD.

Leaf area measurements made on plants at the Plumley Farm in 1999 revealed that leaf area (cm² leaf<sup>-1</sup>) distribution in relation to insertion point (main stem node no.) was distinctly different between the two growth forms (Fig. 7). Leaves derived from the indeterminate meristem of vegetative plants reached similar mature sizes throughout the growing season (40–60 cm² leaf<sup>-1</sup>). The determinate meristem of reproductive

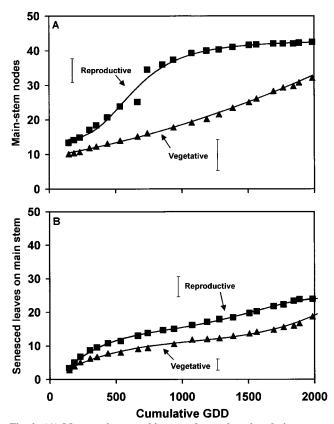


Fig. 4. (A) Mean main-stem chicory node numbers in relation to cumulative growing degree days (GDD) for reproductive ( $\blacksquare$ ; n=40 plants) and vegetative ( $\blacktriangle$ ; n=32 plants) growth forms at the Scott Farm in 1997. Lines represent regression equations for reproductive { $y=29.1/[1+(x/616.0)^{-3.3}]+13.8$ ;  $R^2=0.96$ ; P<0.001} and vegetative { $y=2.09\times10^{-6}x^2+7.4\times10^{-3}x+9.17$ ;  $R^2=0.99$ ; P<0.001} plants. (B) Mean main-stem leaf loss for reproductive ( $\blacksquare$ ; n=40 plants) and vegetative ( $\blacktriangle$ ; n=32 plants) growth forms at the Scott Farm in 1997. Lines represent regression equations for reproductive ( $y=-7.38\times10^{-12}x^4+3.62\times10^{-8}x^3-6.16\times10^{-5}x^2+5.08\times10^{-2}x-2.43$ ;  $R^2=0.99$ ; P<0.001) and vegetative ( $y=5.39\times10^{-9}x^3-1.75\times10^{-5}x^2+.023x+0.37$ ;  $R^2=0.99$ ; P<0.001) plants. Error bars are the pooled standard error of the mean for each growth form.

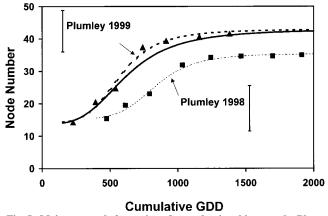


Fig. 5. Main stem node formation of reproductive chicory at the Plumley Farm. Lines are regression equations for 1998  $\{y=20.0/[1+(x/833.7)^{-5.82}]+15.4;\,R^2=0.93;\,P<0.001;\,n=23\,$  plants;  $\blacksquare\}$  and 1999  $\{y=28.6/[1+(x/575.8)^{-4.24}]+14.3;\,R^2=0.96;\,P<0.001;\,n=29\,$  plants;  $\blacktriangle\}$ . The response for the Scott Farm in 1997 (solid line; see Fig. 4 for equation) is included for comparison. Error bars are the pooled standard error of the mean for each year.

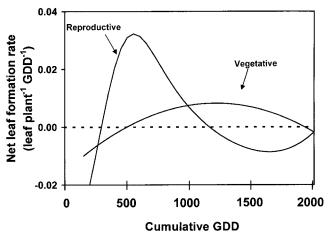


Fig. 6. Net main-stem leaf formation rates of reproductive and vegetative chicory as a function of cumulative growing degree days (GDD) at the Scott Farm in 1997. The lines represent the difference between leaf formation and senescence rates calculated as the first derivatives of the equations for main stem node formation and leaf senescence presented in Figures 4A and 4B.

plants tended to produce large leaves (up to 100 cm²) in early spring (lowest nodes). However, mature leaf size declined rapidly with increasing node number; the uppermost 10 to 15 main stem nodes supported leaves that were <2.5 cm². Total main-stem leaf area (cm² plant¬¹) was also different between the two growth forms. Before bolting, total leaf area averaged 190 cm² plant¬¹ (250 GDD) (Fig. 8). Total leaf area of vegetative plants did not fluctuate much from this initial level across the season. Reproductive plants, however, had total leaf areas that were three times higher than that

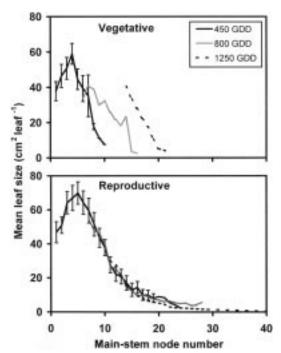


Fig. 7. Mean size of main stem green leaves (n=15 plants) by main stem node number for vegetative and reproductive chicory plants at three dates during the 1999 growing season at the Plumley Farm. Vertical bars ( $\pm$  1 SE of the mean; n=15 plants) are included for data collected at 450 growing degree days (GDD).

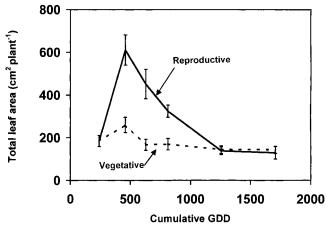


Fig. 8. Mean total main-stem leaf area plant<sup>-1</sup> (n=15 plants) of chicory in vegetative and reproductive plants as a function of growing degree days (GDD) at the Plumley Farm in 1999. Vertical bars are  $\pm$  1 SE of the mean.

of the vegetative plants when measured at 480 GDD due to the high rate of leaf formation between initiation of bolting and first open flower. Total leaf area on reproductive plants then declined as the largest, most basal leaves senesced.

## **DISCUSSION**

Management to optimize forage yield and maintain chicory population in a sward over time requires a comprehensive understanding of the plant's life cycle. During the establishment year, chicory plants had a vegetative growth form with only an occasional reproductive plant observed. However, our data suggest that in subsequent years, both vegetative and reproductive plants commonly co-occur in managed chicory pastures, which presents a dilemma in terms of forage potential for grazing animals. Reproductive plants appear more productive in terms of dry matter yield per plant but are probably lower in forage quality due to their stem content compared with leafy vegetative plants. Reports concerning ruminant utilization of Puna chicory describe livestock preferences for plants that have not bolted (Hunt and Hay, 1990; McCoy et al., 1997). These observations led to recommendations for chicory to be grazed or clipped to maintain plants in the vegetative stage (Barry, 1998). Belesky et al. (1996) observed, however, that sheep may refuse vegetative chicory. Animal selection of herbage is not based on the protein and fiber concentration of the tissue alone but is influenced by other factors such as secondary metabolites that can affect grazer preference (Church, 1979; Rosenthal and Janzen, 1979). Differences in the chemical composition of plant structures, the relative mass of different structures or organs, and the relative number of different structures that a plant produces are important factors in plant survival and herbivory (Bazzaz et al., 1987). Coexistence of reproductive and vegetative growth forms may influence forage utilization by grazing livestock and affect long-term survival of the chicory population, but the mechanisms involved in these relationships are not fully understood.

Chicory populations decline with time, are generally independent of grazing frequency and intensity (Hume et al., 1995; Li et al., 1997b), and decline following grazing in late autumn (Li et al., 1997b). However, Li et al. (1997c) showed in a glasshouse study that cutting height had a significant impact on secondary and axillary leaf masses but no significant impact on secondary stem mass. High rates of N (200 kg ha<sup>-1</sup>) were observed to have a negative impact on chicory regrowth in the subsequent growing season (Clark et al., 1990a; Belesky et al., 2000). Chicory decline could be the result of a bimodal (vegetative and reproductive) development of the crop. Our observations revealed that 33% of the plants died between the 1997 and 1998 growing seasons at the Scott Farm regardless of whether they were vegetative or reproductive the previous year. Surviving plants tended to alternate their growth form. Ninetyfive percent of surviving 1997 vegetative plants switched to a reproductive form in 1998, and 67% of 1997 reproductive plants switched to a vegetative growth form in the subsequent year. These observations suggest that there are management and environment interactions that need to be clarified to understand the impact of management and grazing on chicory production and persistence.

It is likely that differentiation from a vegetative to a reproductive form had already occurred at the meristem level before early spring. Therefore, early grazing or clipping of pastures before 250 GDD (i.e., before initiation of bolting and elevation of the apical meristem) is not likely to remove many meristems or affect the ratio of reproductive to vegetative meristems. Grazing in early spring would allow harvest of leaves that would be lost through senescence if grazing was delayed. However, the impact of leaf removal on subsequent plant developmental dynamics is unknown. Delay of first removal until after 650 GDD would result in reproductive meristems being removed with substantial physiological and morphological impacts to the affected plants. Regrowth may lag as dormant basal buds are stimulated into production after clipping or grazing. In contrast, the apical meristems of vegetative plants would remain intact below the grazing zone and could benefit from the improved light environment following removal of the taller reproductive plants and other competing species. Delay of first clipping to 1500 GDD or later would allow seed ripening and potential reseeding although recruitment rate of new seedlings into established stands has not been documented.

Uncut reproductive plants devoted most of the growing season to the sequential developmental processes of bolting, flowering, and seed set. Performance of calves and 15-mo-old bulls on midreproductive chicory was only acceptable when leaf allowances were 15 to 25 g dry matter kg<sup>-1</sup> live weight d<sup>-1</sup> and high calf or bull live-weight gains occurred on flowering chicory with high residuals where livestock preferentially grazed succulent leaf material and left stem material as residual (Clark et al., 1990b). Flowering chicory may have utility as a maintenance feed for breeding ewes or cows toward the end of lactation or when dry (Clark et al., 1990b).

Rotational grazing with rest periods of 24 d minimized bolting and optimized leaf production (Volesky, 1996). However, flowering plants whose main stem has been removed produce new leaves derived from axially crown shoots. Production of these shoots may ultimately weaken the plant. Li et al. (1997c) showed that root mass decreased as cutting height decreased and that persistence was related to taproot size and storage carbohydrates.

Total main-stem leaf areas plant<sup>-1</sup> were similar in vegetative and reproductive plants early in the season (Fig. 7). Total leaf areas of reproductive plants increased to nearly 3 times that of vegetative plants as a result of rapid leaf expression during bolting. However, the increased leaf area was a short-lived phenomenon, lasting only from the beginning of June to the middle of July as leaves were lost due to senescence. Higher rates of leaf senescence in reproductive plants may be related to reallocating resources in preparation for bolting (high leaf loss in early spring) and to flower and seed production (mid to late season). Senescence in vegetative plants may occur as the oldest (most basal) leaves become shaded by the younger expanding leaves of the rosette. The physiological processes that regulate the transition from a vegetative to a reproductive form are unclear as is the role management may play in modifying the transition.

The indeterminate meristem of vegetative plants is capable of continuous production of new leaves across the growing season. These plants maintain a population of green leaves that range in age and size from newly formed expanding leaves to those that are mature and fully developed. Mature leaf size and total green-leaf area plant<sup>-1</sup> of undefoliated, vegetative plants is relatively constant across the season because senesced older leaves are constantly replaced by new growth. Leaf area (mass) removal would likely be maximized by a first harvest between 400 and 500 GDD because harvest at this time would capture the large, fully developed basal leaves of reproductive plants before they senesce. Leaf/ stem ratio and forage quality would likely be high at this time as well. Management strategies that result in shifting the population toward vegetative plants may improve the seasonal distribution of forage because the indeterminate meristems of vegetative plants continue to produce leaves over the growing season.

Because total leaf areas for vegetative and reproductive plants were similar (except during bolting), the question could be asked, why remove stems by early grazing or clipping? One possible answer may be related to the forage quality of the elevated leaves. Forage quality, preference, and palatability may be responsible for lowered grazing intake and animal performance. The phenological model and leaf initiation data presented in this study can serve as a framework with which to evaluate changes in the quality of chicory forage. The relationships among plant development, forage yield, and forage quality will have to be understood to improve utilization of chicory in permanent pastures. The complex bimodal population structure and plant development relationships of chicory suggest that models may

prove to be an invaluable tool for developing efficient management strategies to capitalize on the ability of chicory to produce under marginal conditions.

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